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Effects of Velocity and Limb Loading on the Coordination Between Limb Movements During Walking

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ABSTRACT. The authors investigated the effects of velocity (increasing from 0.5 to 5.0 km/hr in steps of 0.5 km/hr) and limb loading on the coordination between arm and leg movements during treadmill walking in 7 participants. Both the consistency of the individual limb movements and the stability of their coordination increased with increasing velocity; the frequency coordination between arm and leg movements was 2:1 at the lower velocities and 1:1 at the higher velocities. The mass manipulation affected the individual limb movements but not their coordination, indicating that a stable walking pattern was preserved. The results differed qualitatively from those obtained in studies on bimanual interlimb coordination, implying that the dynamical principles identified therein are not readily applicable to locomotion.

Key words: asymmetry, interlimb coordination, load, stability, walking

In the past two decades or so, the dynamical systems approach, in particular Haken's (1983) synergetics, has been applied quite successfully in the study of coordinated movements, especially rhythmic ones. That line of research was initiated by experiments on phase transitions in rhythmic finger and hand movements (Kelso, 1981, 1984) and their theoretical analysis (Haken, Kelso, & Bunz, 1985). The experiments in question demonstrated that (a) interactions between rhythmically coordinated finger movements result in attraction to one of two coordination modes (i.e., in-phase and antiphase); (b) those modes are differentially stable in that at sufficiently low movement frequencies the performance of the in-phase coordination is more stable than that of the antiphase coordination; and (c) the stability of coordination decreases with increasing movement frequency, eventually resulting in a loss of stability of the antiphase coordination followed by an abrupt transition to the in-phase coordination. Those observations were corroborated for other limb pairs involving the legs (Jeka, Kelso, & Kiemel, 1993). An important conceptual and operational merit of the dynamical systems approach to coordinated movement is that it showed that patterns of rhythmic interlimb coordination can be captured in terms of a single macroscopic variable or order parameter, namely, the relative phase between the limb movements, allowing for a compact, rigorous description and examination of the stability properties of such patterns.

Following the success of the dynamical systems approach in identifying the stability features of rhythmic interlimb coordination, researchers extended the obtained insights to instances in which the individual components are asymmetrical, for instance, as a result of anthropomorphic differences such as between arms and legs (cf. Baldissera, Cavallari, & Civaschi, 1982; Carson, Goodman, Kelso, & Elliott, 1995; Daffertshofer, Van den Berg, & Beek, 1999; Fuchs, Jirsa, Haken, & Kelso, 1996; Jeka et al., 1993; Kelso & Jeka, 1992; Schmidt, Shaw, & Turvey, 1993; Schöner, Jiang, & Kelso, 1990; Swinnen, Dounskaia, Verschueren, Serrien, & Daelman, 1995; Swinnen, Jardin, Meulenbroek, Dounskaia, & Hofkens-Van den Brandt, 1997; Treffner & Turvey, 1996). For such asymmetrical cases, the researchers formulated useful model extensions that capture the relative phase dynamics. Parallel to that development, they sought generalization of the identified basic principles of coordination dynamics in the context of more naturally occurring behaviors, such as human locomotion (e.g., Van Emmerik & Wagenaar, 1996; Whitall, 1989; Whitall & Caldwell, 1992). In fact, several basic experiments on interlimb coordination were motivated by the idea that human locomotion can be

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typified as pendular, "clocking" movements and that one can study the organizational principles of such movements by having people swing hand-held pendulums about the wrists (cf. Kugler & Turvey, 1987; Peck & Turvey, 1997). In a similar vein, Kelso's experiments on finger and hand movements were inspired by the advertising slogan "Let your fingers do the walking" (Kelso, 1995, p. 46). To what extent, however, are rhythmic arm and hand movements suitable model systems for studying principles of locomotion? Or, framed differently, how universal are the coordination principles identified in the basic modeling experiments, and, in particular, are they applicable to locomotion?

Although it has been amply demonstrated that coordinated rhythmic behavior can be described in terms of nonlinear oscillations of the participating body segments with properties that are largely independent of structural peculiarities (e.g., Cohen, Holmes, & Rand, 1982), it is still largely unclear how the physical properties of effector systems affect or shape the coordination dynamics. Indeed, Kelso designed his finger experiments to examine issues of relative timing in their purest possible form by minimizing the role of mechanical factors (cf., e.g., Schöner, 1995) that may have much stronger effects in tasks requiring coordination of two or more whole limb movements (cf. Jeka et al., 1993; Kelso & Jeka, 1992). In all likelihood, mechanical constraints play an even more prominent role in walking because walking requires the preservation of dynamic balance and, hence, stable yet flexible patterns of interlimb coordination.

Although different gait patterns, such as walking and running, have been successfully described in terms of phase relations, some marked differences with the results of studies on bimanual coordination have been reported. For instance, whereas coordinative stability is inversely related to movement frequency in bimanual coordination tasks, that relationship is reversed in human locomotion (Craik, Herman, & Finley, 1976; Wagenaar & Van Emmerik, 1994, 2000). Furthermore, the differential stability of in-phase and antiphase coordination in bimanual tasks has not been observed during walking. That is, during walking, no significant differences in coordinative stability between ipsilateral arm and leg movements (antiphase) and contralateral arm and leg movements (in-phase) have been found (Donker, Beek, Wagenaar, & Mulder, 2001). Thus, the following question arises: To what extent can the coordination principles identified in "pure" coordination experiments, such as Kelso's (1981, 1984) experiments on finger movements, be applied to situations in which mechanical constraints play a more prominent role? The importance of that question is amplified by the theoretical consideration that, during evolution, the specific selective pressures (e.g., balance, energy cost) have molded the neural organization of the control of the lower limbs in a markedly different way from that of the upper limbs (cf., e.g., Riek & Carson, 2001).

Especially in light of the current upsurge of interest in the dynamical systems approach as a framework for studying both naturally occurring behavior and movement pathologies (cf. Dingwell, Cusumano, Sternad, & Cavanagh, 2000; Mackey & Milton, 1987; Scholz, 1990; Wagenaar & Van Emmerik, 1994), it has become pertinent to examine in detail how the (allegedly general) organizational principles of coordination dynamics are affected by the prevailing task constraints. Our goals in the present study were (a) to examine in what manner the coordination between limb movements during walking at a range of velocities is affected by mechanical factors in the form of limb loading and (b) to critically compare the results with those of previous studies regarding the effects of tempo (movement frequency) and asymmetry on human interlimb coordination.

Our experimental setup was inspired in part by Jeka and Kelso's (1995) study on the coordination between arm and leg movements. In Jeka and Kelso's study, participants sat in a specially designed chair and moved their arms and legs in either in- or antiphase. A mass was attached to their wrist or ankle, thereby increasing or decreasing the symmetry between the limbs. In the present study, we applied essentially the same mass manipulation as was used by Serrien and Swinnen (1998), thus allowing for a direct comparison with the coordination dynamics observed in more formal modeling studies on interlimb coordination. Whereas the studies of Jeka and Kelso and Serrien and Swinnen involved tasks with no (or small) mechanical interactions with the environment, our concern in the present study was with the patterns of interlimb coordination observed in a naturally occurring behavior in which mechanical constraints on interlimb coordination are much more prominent: namely, human walking.

Method

Participants

Four women and 3 men (mean age = 27 years; range = 21–37 years) volunteered to participate in the experiment. All participants were healthy and did not suffer from any motor impairments or movement-related disorders. They were all naive with regard to the purpose of the experiment. After the local Medical Ethics Committee had approved the experiment, all participants gave their written informed consent before their participation.

Recordings

The participants walked on a walking belt (Enraf Nonius, Delft, The Netherlands, Model Entred Reha) at a computer-controlled velocity. We determined angular displacements of left and right forearms and lower legs by using small lightweight triangular frames carrying a reflective spherical marker (diameter 20 mm) on each corner (Figure 1A). We recorded their positions at a sampling rate of 100 Hz by means of a three-dimensional (3D) passive registration system called *PRIMAS* (Furnée, 1989), consisting of six video cameras and a control unit. The 3D reconstruction error of the positions of the markers was about 1 mm. In the present study, the analysis of the limb movements was confined to the sagittal plane (see Figure 1).

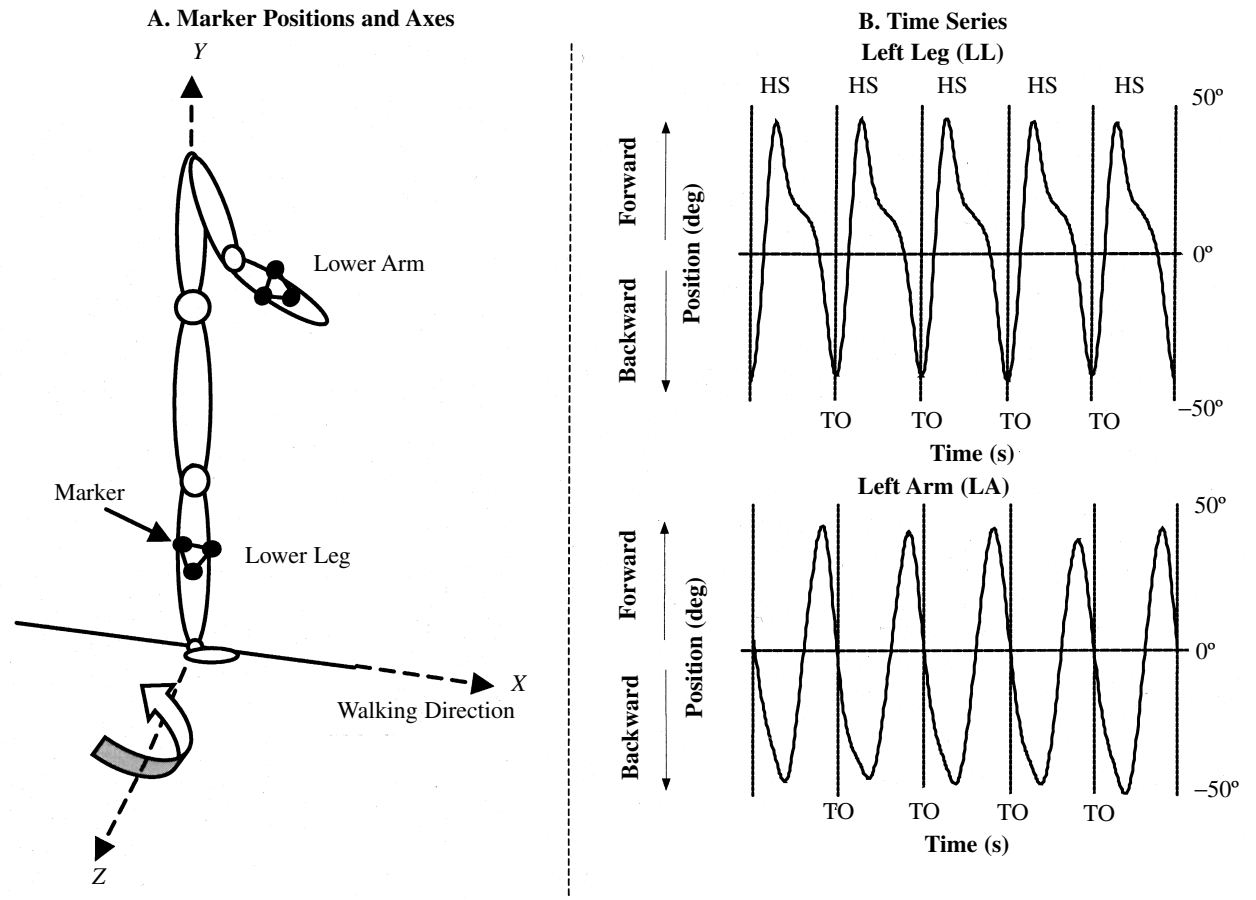

FIGURE 1. A. Sagittal view of the marker configuration (black circles) and the *x*-, *y*-, and *z*-coordinate axes. Marker frames (each holding three markers) were placed on the forearms and lower legs. The sagittal plane is the *x*,*y* plane. The focus in the present study was on the rotational movements (in degrees) of the limbs around the *z*-axis (i.e., in the sagittal plane). **B.** Example of the rotational movements of left leg and left arm. Stride cycles were defined by the moments of maximal backward movement (or toe-off, TO) of the left leg. The moments of maximal forward leg movement corresponded to heel strike (HS).

Procedure

Each participant took part in a single measurement session consisting of four conditions: (a) a control condition in which no mass was attached to the limbs (NL), and three load conditions in which a mass was attached (b) to both arms (LBA), (c) to the right arm (LRA), or (d) to the right leg (LRL). Following Jeka and Kelso (1995), we placed wristbands filled with 1.8 kg of sand at the distal ends of the limbs (i.e., wrist or ankle) to either reduce the symmetry between homologous limbs (LRA and LRL) or enhance the symmetry between nonhomologous limbs (LBA). Although we applied no randomization algorithm, we were careful that the order in which the experimental load conditions were applied differed across participants.

Before the start of the experiment, we took a reference measurement during which we recorded the position of the walking belt and the positions of the marker frames for future reference. Before each experimental load condition, the participant became acquainted with the experimental condition in question by walking at different walking velocities for 2 to 5 min. Each load condition consisted of one long trial during which the belt velocity was gradually increased from 0.5 km/hr up to 5.0 km/hr in increments of 0.5 km/hr. About 15 s after changing the velocity of the walking belt, we recorded the position of the markers for 40 s at that particular belt velocity. An entire trial lasted about 10 min. Participants were instructed to walk as naturally as possible. No specific instructions were given with regard to the arm movements.

Data Preprocessing

We defined a three-dimensional Cartesian coordinate system (*x*-, *y*-, and *z*-axes) on the basis of the reference measurements (Figure 1A). The arm and leg movements were expressed as rotations (in degrees) around the horizontal axis (i.e., in the sagittal plane), with increasing values corresponding to forward movements and decreasing values to backward movements (cf. Figure 1B). Using a second-order Butterworth low-pass filter with a cut-off at 5 Hz, we filtered the rotational movements. For each walking velocity and load condition, we used seven consecutive stride cycles

for analysis. We defined a stride cycle by the moments of maximal backward movements of the left lower leg—that is, starting and ending with toe-off of the left leg (see Figure 1B, upper panel, for an example). We determined the valleys and peaks in the angular displacement signals by means of a peak-detection algorithm.

First, we analyzed the individual limb movements in terms of their consistency (or variability). Subsequently, we examined the frequency coordination between the arm and leg movements to separate the trials in which the dominant movement frequencies of the different limbs were (nearly) identical from those in which the dominant frequency of the arm movements differed from that of the leg movements. The results of that analysis determined the choice for the subsequent processing steps aimed at identifying persistent frequency and phase relations as well as the stability of those relations. For that purpose, we adopted two conventional measures for spectral analysis, namely, coherence and Fourier phase, which we appropriated to the coordination issues of interest. In brief, coherence represents the cross-correlation between spectral components of two signals. Because the present focus was on specific frequency ranges around the frequencies of the limb movements, we used a slightly modified measure called the *weighted coherence* (Porges & Bohrer, 1980; see *Analysis of Interlimb Coordination*). Coherence analysis requires that the two input signals possess significant spectral power at common frequencies; that is, the dominant movement frequencies should be largely identical, implying that arms and leg movements have to be 1:1 frequency locked. The *Fourier phase* refers to the timing of a given spectral component in a signal; that is, every harmonic (or Fourier component) in a periodic signal is associated with a certain phase. Provided that this phase is calculated over a finite time window for every frequency, one can analyze its change over time. After calculating the time-varying Fourier phase for two signals at selected frequencies in that manner, one can calculate the time-dependent, continuous relative Fourier phase at those frequencies, even if they are different (see the following sections). For that reason, one can always calculate the relative Fourier phase regardless of the frequency ratio between the limb movements (i.e., be it 1:1 or 2:1). Like the point estimate and the continuous estimate of relative phase as commonly used in the literature on interlimb coordination, the (continuous) relative Fourier phase provides insight into eventual coordination modes and their stability. Notice that the weighted coherence combines amplitude and phase effects, whereas the relative Fourier phase solely reflects changes in phase dynamics, so one can disentangle amplitude and phase effects by comparing both measures in the isofrequency case.

Analysis of the Individual Limb Movements

Consistency of movement trajectories. We examined the consistency of the angular limb trajectories during the stride cycle as follows. First, we normalized the duration of the stride cycles of the limb trajectories to 100% on the basis of the shortest stride duration of all trials and scaled the amplitude of the limb trajectories to 1.0. For each walking velocity, we calculated the average of the thus-normalized limb angle trajectory of the control condition (NL) over seven subsequent stride cycles and used that result as the reference trajectory for all load conditions. Subsequently, for each walking velocity and load condition, we estimated the difference between the reference trajectory and the normalized limb angle trajectories by calculating the squared distance between the two signals at each sampled point of the normalized stride cycle. Finally, we summed those squared distances, divided them by 100, and then calculated the root (i.e., a root mean squared difference), which resulted in a measure for the consistency of the limb movements over the different load conditions as compared with the control condition. (For a more detailed analysis of the influence of mass on the individual arm and leg movements and the muscle activity of the arms, we refer to Donker, Nienhuis, Mulder, & Duysens, 2002.)

Analysis of Interlimb Coordination

Spectral analysis. For the position data of each limb movement, we determined the power spectral density (Welch's periodogram method, in which a Hamming window of half the length of the movement trajectory is used [Chatfield, 2003]), and defined the location of the largest spectral power as the dominant frequency of the limb movement. To examine the frequency locking between ipsilateral arm and leg movements, we calculated the ratio between their dominant frequencies at each side of the body. We assumed that frequency locking was present if those ratios (almost) equaled 1:1 or 2:1 (allowing a deviation of ±0.1 from the ratios of interest, i.e., 1:1 and 2:1; for further details, see Donker et al., 2001).

To determine the coupling strength between limb movements (i.e., shared rhythmicity) within the domain of the dominant movement frequency, we calculated the weighted coherence (Porges & Bohrer, 1980) for all limb pairs. The weighted coherence, or C_w, was calculated across a frequency band of ±0.15 centered around the dominant frequency of limb x (ω_x) according to

$$C_w = \frac{\int_{\omega_x-0.15}^{\omega_x+0.15} C_{xy}(\omega)\cdot P_x(\omega)d\omega}{\int_{\omega_x-0.15}^{\omega_x+0.15} P_x(\omega)d\omega}.$$

$C_{xy}(\omega)$ denotes the coherence between signals x and y, and $P_x(\omega)$ symbolizes the power spectral density of signal x at frequency ω. In the case of nonhomologous limb pairs, we used the leg movement as reference x, whereas in the case of homologous limb pairs, we used the left limb for that purpose. The weighted coherence was calculated between limb movements with the same dominant frequency. As a

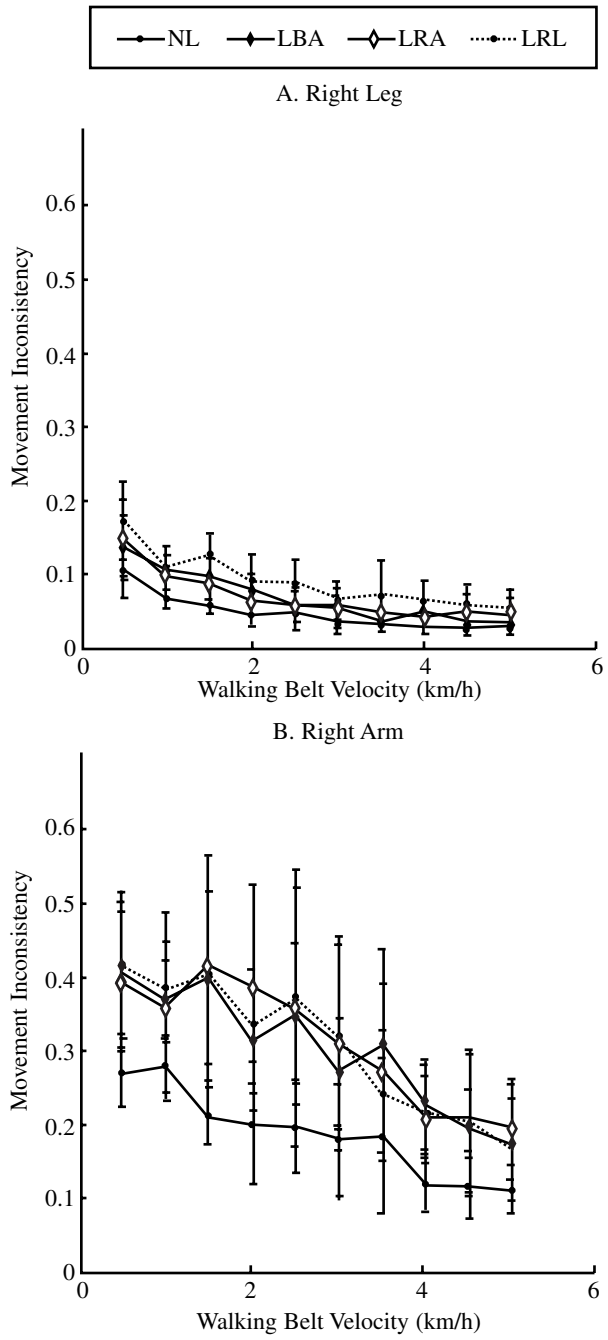

FIGURE 2. The mean values for the consistency of right leg (**A**) and arm (**B**) trajectories averaged over the 7 participants are presented for all four load conditions as a function of walking velocity. The higher the value, the more the movement trajectory differs from the reference (i.e., no load) movement trajectory, that is, the greater the variability of the movement trajectory. The error bars (i.e., ± 1 *SD*) represent the intersubject variability. The figures for the mean values for the consistency of the left leg and arm trajectories were very similar to those depicted for the right leg and arm trajectories and were therefore omitted. NL = no load; LBA = load on both arms; LRA = load on right arm; LRL = load on right leg.

consequence, we calculated the weighted coherence between the right and left leg movements (RL/LL) for all walking velocities; for other limb pairs, we restricted that analysis to the velocity range 3.0 to 5.0 km/hr (see Results).

Continuous relative Fourier phase. In general, especially because of the forceful impact of the feet with the floor, the continuous estimates of the relative phase between limb movements during walking are influenced by higher harmonic components in the trajectories (cf. Post, Daffertshofer, & Beek, 2000, for similar phenomena in juggling). One can eliminate those effects by calculating the difference between the continuous Fourier phases of the dominant frequencies in the limb trajectories (Lamoth, Beek, & Meijer, 2002). The calculation of the relative Fourier phase proceeded as follows. First, we determined the dominant frequency in the limb trajectories as just discussed. Second, we used a windowed Fourier transform to determine the Fourier phase of that dominant frequency at each sample of the time series (similar to the computation of the spectrogram), resulting in a continuous estimate of the phase at the dominant movement frequency. The length of the time window was chosen as twice the period of that dominant frequency. Third, we calculated the continuous relative Fourier phase for the six limb pairs of interest by subtracting the Fourier phases of the individual limb movements according to

$$\theta_{n:m} = n\varphi_S - m\varphi_F,$$

where *n:m* represents the previously defined frequency ratios. For example, in the case in which *n:m* is 2:1, φ_S represents the slower limb (i.e., with dominant frequency ω_0) and φ_F the faster limb (i.e., with dominant frequency $2\omega_0$; see also Sternad, Turvey, & Saltzman, 1999).

In contrast to the weighted coherence measure, we included all trials in that analysis. We calculated both intratrial means and standard deviations (*SD*s) of the relative Fourier phase by using circular statistics (cf. Batchelet, 1981; Burgess-Limerick, Abernethy, & Neal, 1991).

Statistical Analysis

Using SPSS (SPSS, Inc., Chicago, IL), we performed separate repeated measures analyses of variance (ANOVAs) on the dependent measures mentioned in the preceding, using a factorial design involving three within-participants factors: (a) load (4 levels, i.e., NL, LBA, LRA, and LRL); (b) walking velocity (10 levels, i.e., 0.5 to 5.0 km/hr in steps of 0.5 km/hr); and (c) limb (4 levels, i.e., left arm [LA], right arm [RA], left leg [LL], and right leg [RL]) when analyzing individual limb movements, or limb pairs (6 levels, i.e., RL/LL, LA/RA, LA/LL, RA/RL, LA/RL, and RA/LL) when analyzing interlimb coordination. For the dependent measure weighted coherence, we reduced the within-participants factor walking velocity from 10 to 5 levels (i.e., 3.0 to 5.0 km/hr in five steps of 0.5 km/hr) because only at those velocities did all limb movements have common dominant frequencies. Because the dominant frequencies between both legs were equal at all walking velocities, we performed an addi-

tional repeated measures ANOVA on weighted coherence for the limb pair involving the within-participants factors load (4 levels) and walking velocity (10 levels). To evaluate any significant findings, we performed post hoc pairwise comparison analyses with a Bonferroni correction of the p value based on the number of comparisons (α level of .05).

Results

In the following, we first report the effects of limb (i.e., arm versus leg), walking velocity, and limb loading on the consistency of the individual limb movements and then the effects of limb pair, walking velocity, and limb loading on the frequency and phase coordination between the limb movements as observed in all six pairs of limb movements (i.e., RL/LL, LA/RA, LA/LL, RA/RL, LA/RL, and RA/LL).

Consistency of the Individual Limb Movements

Effect of Limb

The difference from the reference trajectory (i.e., no-load condition) was significantly smaller for leg movements than for arm movements, $F(3, 18) = 312.4$, $p < .001$, indicating that leg movements were more consistent than arm movements (see Figure 2).

Effect of Walking Velocity

The difference between the individual limb movements and the reference trajectory decreased significantly with increasing walking velocity, $F(9, 54) = 26.7$, $p < .001$, indicating that the variability of the limb movements decreased with increasing walking velocity (see Figure 2). Moreover, a significant interaction effect between velocity and limb, $F(27, 162) = 4.2$, $p < .001$, revealed that the difference between arm and leg movements decreased with increasing walking velocity.

Effect of Load

As is apparent from Figure 2, the added mass significantly affected the consistency of the movements of all four limbs in comparison with that in the no-load condition, $F(3, 18) = 21.1$, $p < .001$. The effect was stronger for arm than for leg movements, as was evident from a significant interaction effect between limb and load, $F(9, 54) = 8.2$, $p < .001$.

Interlimb Coordination

Spectral Analysis

The spectral analysis of ipsilateral arm and leg movements revealed that at low walking velocities the frequency of the arm movements was, in general, twice as high as that of the leg movements (i.e., the frequency ratio between arm and leg movements was 2:1), whereas at higher walking velocities the arms and legs always moved in unison (i.e., a frequency ratio between arm and leg movements of 1:1; see Figure 3 for an example). Only 9 of the 560 (7 participants × 10 velocities × 4 load conditions × 2 body sides) calculated frequency ratios differed more than 0.1 from 1:1 or 2:1 (all at walking velocities below 2.0 km/hr and randomly distributed across conditions), implying that, on the criterion used, 98.4% of the observed frequency patterns were frequency locked. In 6 of the 7 participants, a 2:1 frequency ratio was observed between ipsilateral arm and leg movements at walking velocities lower than 3.0 km/hr. In 1 participant, the 1:1 frequency coordination was observed at all walking velocities. The frequency coordination patterns observed in all participants except one were more or less constant over the different load conditions. In other words, adding a mass to both arms (LBA) did not decrease the critical walking velocity at which a shift from 2:1 to 1:1 frequency coordination occurred; nor did either of the other two manipulations (LRA and LRL) systematically affect that critical velocity. Group analyses, which revealed no significant effect of load, confirmed that observation, demonstrating that altering the degree of symmetry between the limb movements did not affect their frequency coordination.

The weighted coherence analysis indicated that leg movements were more strongly coupled than were both the arm movements and the arm and leg movements, $F(5, 30) = 6.7$, $p < .001$ (see Figure 4). Collapsed over all limb pairs and load conditions, the weighted coherence increased with increasing walking velocity, $F(4, 24) = 8.3$, $p < .001$. An additional weighted coherence analysis for the leg movements, involving all 10 walking velocities, revealed that the coupling between the leg movements increased significantly with increasing walking velocity, $F(9, 54) = 40.5$, $p < .001$ (see Figure 4). The coupling between the limbs, as indexed by the weighted coherence, was not affected by the different mass manipulations; that is, we found no significant differences between the four experimental load conditions (Figure 4).

Continuous Relative Fourier Phase

Effect of Limb Pair

As expected, the continuous relative Fourier phase differed for the six limb pairs, $F(5, 30) = 54.8$, $p < .001$ (cf. Figure 5). At walking velocities higher than 2.5 km/hr, ipsilateral arm and leg movements (LA/LL, RA/RL) tended to in-phase coordination, and contralateral arm and leg movements (LA/RL, RA/LL) to antiphase coordination. The homologous limb pairs (i.e., arms and legs) both moved in antiphase. Except for RL/LL, those coordination patterns were affected by walking velocity, as is discussed next.

Effect of Walking Velocity

Increasing walking velocity significantly modified the coordination between limb movements, $F(9, 54) = 15.3$, $p < .001$. Specifically, the relative phase between arm movements (LA/RA) and between the ipsilateral arm and leg movements (LA/LL, RA/RL) evolved from a tendency to move in-phase at 0.5 km/hr to a more or less antiphase coordination at 5.0 km/hr. The relative phase between contralateral arm and leg movements (LA/RL, RA/LL) increased with increasing walking velocity at the lower walking velocities but began to decrease to values closer to 0° at velocities

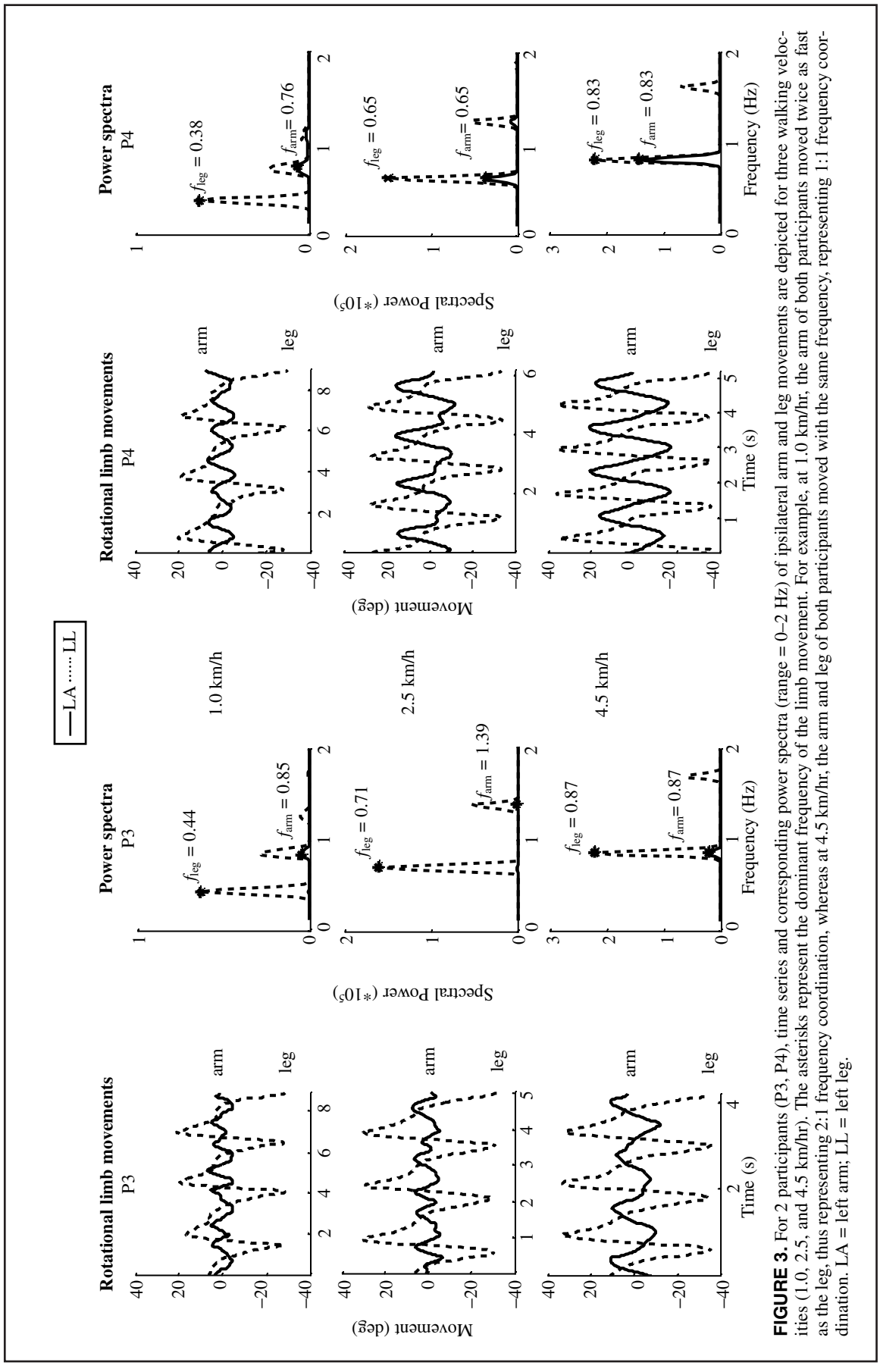

FIGURE 3. For 2 participants (P3, P4), time series and corresponding power spectra (range = 0–2 Hz) of ipsilateral arm and leg movements are depicted for three walking velocities (1.0, 2.5, and 4.5 km/hr). The asterisks represent the dominant frequency of the limb movement. For example, at 1.0 km/hr, the arm of both participants moved twice as fast as the leg, thus representing 2:1 frequency coordination, whereas at 4.5 km/hr, the arm and leg of both participants moved with the same frequency, representing 1:1 frequency coordination. LA = left arm; LL = left leg.

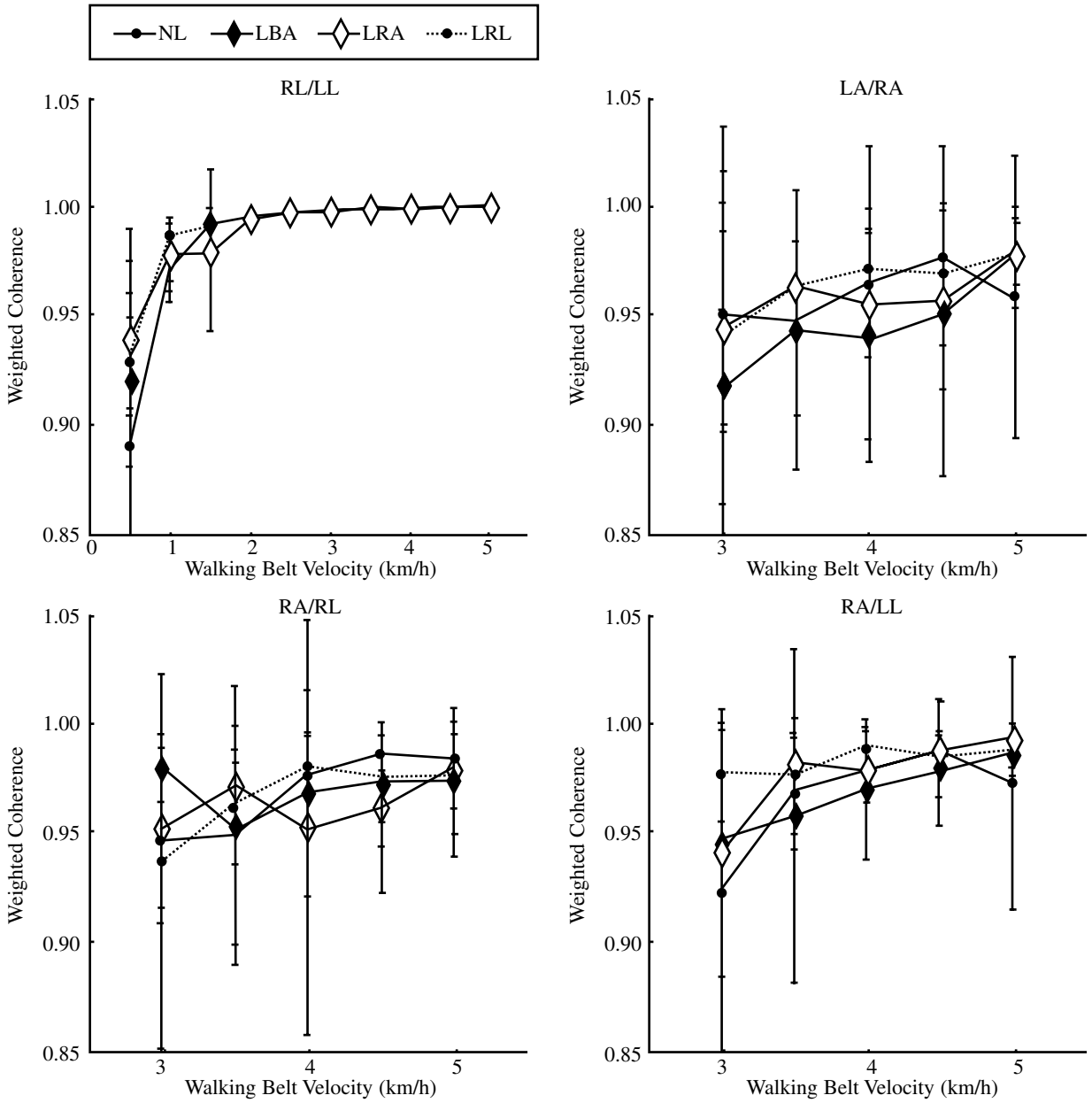

FIGURE 4. The weighted coherence averaged across all participants is shown for all four load conditions for RL/LL, LA/RA, RA/RL, and RA/LL. For walking velocities higher than 2.5 km/hr, all limbs moved at the same frequency, and the weighted coherence could be calculated. Consequently, only the higher walking velocities (i.e., 3.0–5.0 km/hr) are depicted, except for LL/RL, because the dominant frequencies of the legs were equal at all walking velocities. The error bars (i.e., ± 1 *SD*) represent the intersubject variability. RL, LL, LA, and RA = right and left legs and left and right arms, respectively. *SD* = standard deviation.

higher than 2.0 km/hr. However, as can be appreciated from Figure 3, defining the coordination between arm and leg movements during 2:1 frequency coordination as in-phase coordination is somewhat arbitrary because the first valley of the faster limb coincided with the peak of the slower limb (i.e., antiphase), whereas the second valley occurred at half a period after the peak of the slower limb (i.e., in-phase).

On the basis of the observed effects of walking velocity on the coordination between the arm movements (LA/RA; see Figures 3 and 5), one can make a distinction between lower (0.5–1.5 km/hr), intermediate (2.0–2.5 km/hr), and higher (3.0–5.0 km/hr) walking velocities. At the lower velocities, the arms moved in phase and twice as fast as the legs, whereas at the higher velocities, the arms moved in antiphase at essentially the same frequency as the legs. At the intermediate velocities, the 2:1 frequency coordination between arm and leg movements was still present but no longer prevailed because the arms already tended to move

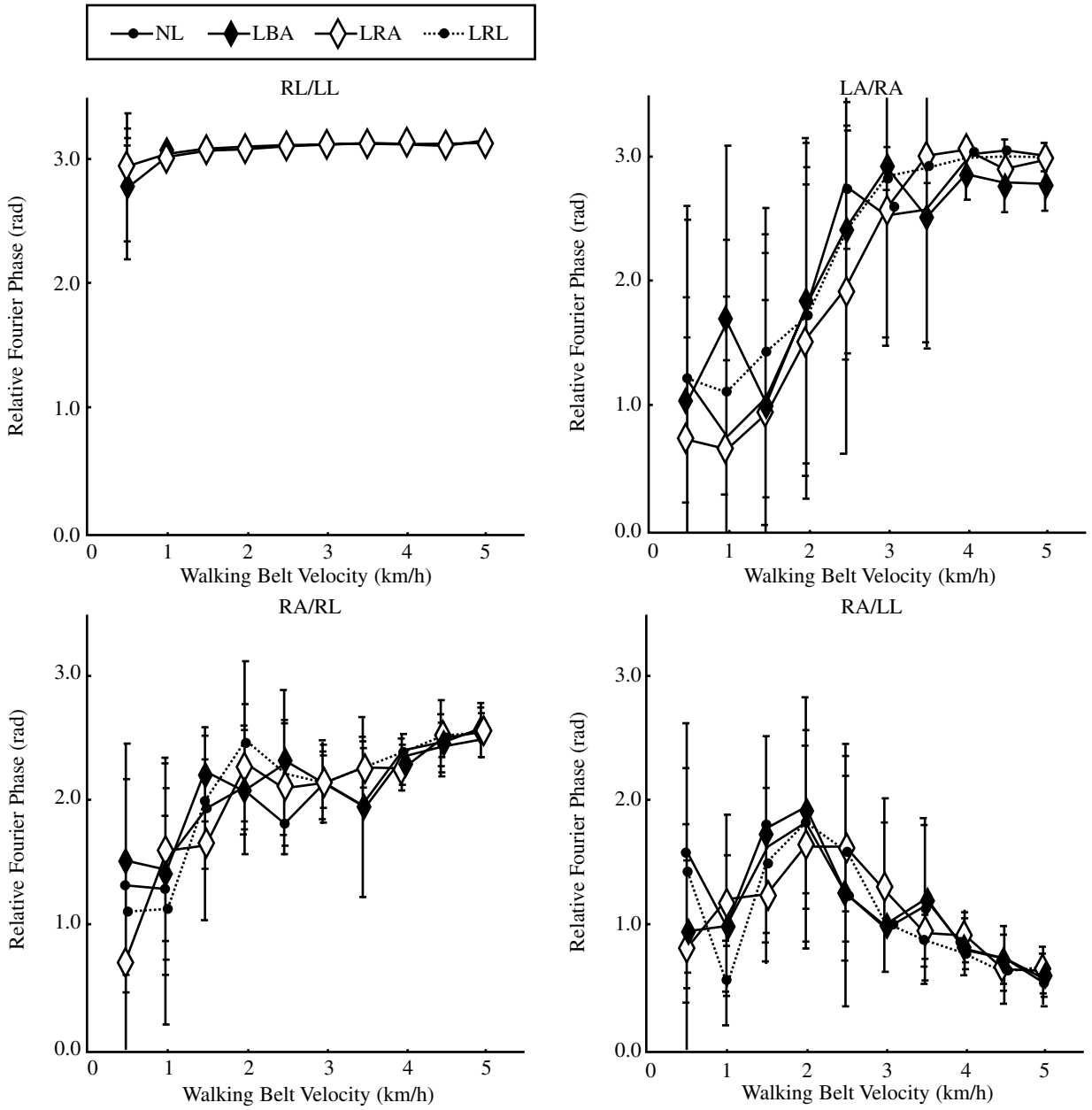

FIGURE 5. Averaged across all participants and for all four load conditions, the mean relative Fourier phase is depicted as a function of walking velocity for the two homologous limb pairs, right and left legs (RL/LL) and left and right arms (LA/RA), respectively; the ipsilateral limb pair, right arm/right leg (RA/RL); and the contralateral limb pair, right arm/left leg (RA/LL). The error bars (i.e., ± 1 *SD*) represent the intersubject variability. *SD* = standard deviation.

in antiphase at the same frequency as the legs. Additional statistical tests revealed a significant effect of velocity for all limb pairs when we restricted the analysis to the lower and intermediate velocities (i.e., 0.5–2.5 km/hr) and when we included only the higher velocities (i.e., 3.0–5.0 km/hr). That finding indicates that the observed effect of walking velocity is genuine and cannot solely be explained by a change in frequency coordination.

Effect of Load

No significant effects of load were found (Figure 5), which confirmed the results obtained for the analysis of the frequency coordination between the limb movements, indicating that neither increasing nor decreasing the degree of symmetry between the limbs affected interlimb coordination during walking.

Variability of Continuous Relative Fourier Phase

Effect of Limb Pair

When we collapsed limb pair over load conditions, we found a significant effect, $F(5, 30) = 23.7$, $p < .001$, on the *SD* of the relative Fourier phase. That is, in all load conditions and at all velocities, the *SD* of the Fourier phase between the legs (RL/LL) was smaller than were those for the other five limb pairs in the absence of any significant differences among the remaining five limb pairs. That result is consistent with that obtained for the weighted coherence.

Effect of Walking Velocity

As can be appreciated from Figure 6, the *SD* of the relative Fourier phase decreased with increasing walking velocity for all limb pairs, $F(9, 54) = 22.4$, $p < .001$, suggesting that the stability of interlimb coordination increased with increasing walking velocity and corroborating the findings

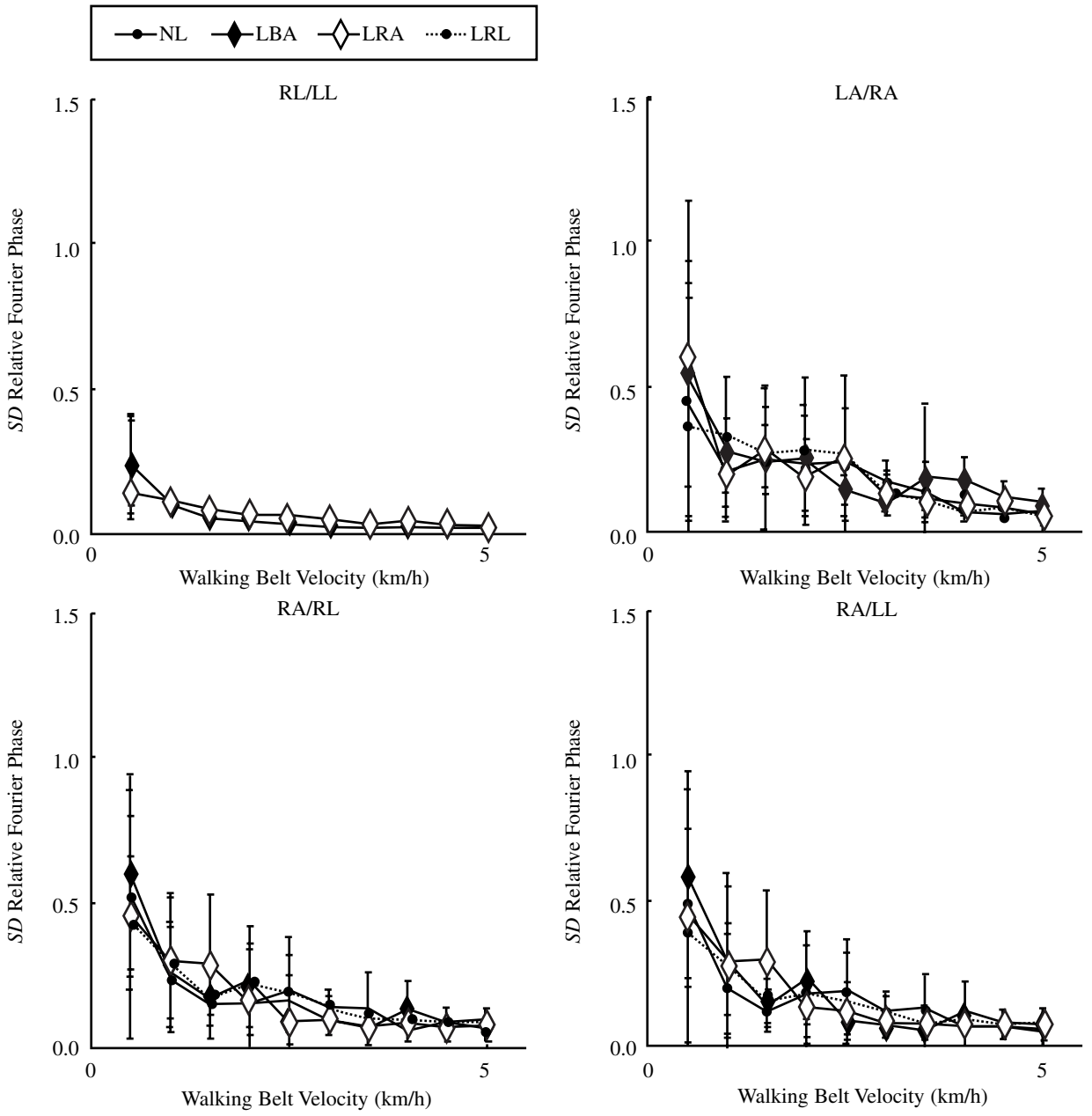

FIGURE 6. The *SD* of the relative Fourier phase between right and left legs (RL/LL), left and right arms (LA/RA), right arm and leg (RA/RL), and right arm and left leg (RA/LL) is depicted for each experimental load condition as a function of walking velocity. The error bars (i.e., ± 1 *SD*) represent the intersubject variability. NL, LBA, LRA, and LRL = no-load, load on both arms, load on right arm, and load on right leg conditions, respectively. *SD* = standard deviation.

of the weighted coherence analysis. Additional statistical tests further revealed that the effect of walking velocity remained significant when only the 0.5–2.5 km/hr or the 3.0–5.0 km/hr velocity range was included, implying that the observed effects of walking velocity were not primarily related to the change in frequency coordination between arm and leg movements from 2:1 to 1:1.

Effect of Load

We found no significant effect of load (Figure 6), confirming the results of the weighted coherence in that neither enhancing the symmetry between nonhomologous limbs (LBA) nor reducing the symmetry between homologous limbs (LRA and LBA) affected the stability of interlimb coordination.

Summary of the Main Results

1. The variability of all four individual limb movements (see Figure 2) decreased with increasing walking velocity, as did the variability of the relative phasing between the limb movements in all six limb pairs (see Figure 6).
2. The variability of the leg movements was smaller than that of the arm movements, and that difference became smaller with increasing walking velocity (see Figure 2).
3. Adding mass to an arm or leg affected the consistency of movement of the loaded limb, especially in the arms (Figure 2).
4. In contrast, adding mass to an arm or leg (i.e., changing symmetry) had no effect on the observed coordination patterns (see Figure 5) or their stability (see Figures 4 and 6).
5. Similarly, no differences in coordinative stability were found between in-phase and antiphase arm and leg movements (Figure 6). In the following section, we compare those results with the results of previous studies on interlimb coordination and discuss the theoretical implications of that comparison.

Discussion

Inspired by the advent of the dynamical systems approach as an expedient conceptual framework for studying human movement—in particular rhythmic interlimb coordination—we examined whether, and to what extent, known principles of rhythmic interlimb coordination dynamics also apply to everyday cyclical motor activities—in particular, human walking. Stated differently, we were interested in uncovering how the prevailing, putatively largely mechanical, task constraints of walking affect the dynamics of interlimb coordination during locomotion. To that aim, we studied the effects of limb loading and walking velocity on interlimb coordination during treadmill walking.

The results we obtained differed in three important ways from the insights typically gained from experimental studies on the relative phase dynamics of coordinated behavior aimed at developing and testing formal model constructs. First, coordinative stability (as indexed by weighted coherence and the *SD* of the relative Fourier phase) was positively related to (walking) velocity (see Figures 4 and 6), rather than inversely (cf., e.g., Kelso, 1981, 1984). Second, we found no differences in stability between in-phase (i.e., RA/RL and LA/LL) and antiphase (i.e., RA/LL and LA/RL) movements, rather than evidence that those two modes are differentially stable (cf., e.g., Baldissera, Cavallari, Marini, & Tassone, 1991; Kelso, 1984; Zanone & Kelso, 1992). Third, the coupling between nonhomologous limb movements (i.e., arm and leg movements) was similar to that between homologous limb movements (i.e., arm movements) also in the case of asymmetrical loading (i.e., LRA and LRL; see Figure 6). Moreover, loading both arms (LBA), and thus reducing the physical differences between arms and legs, had no significant effect on either frequency or phase coordination between arm and leg movements (Figure 5) or on coordinative stability (Figures 4 and 6), contrary to the results of previous studies (cf., e.g., Kelso & Jeka, 1992). The first two results replicate previous findings on interlimb coordination during walking (Craik et al., 1976; Donker et al., 2001; Wagenaar & Van Emmerik, 1994) and can at least be partially explained by the specific task constraints of human walking, such as the forceful impact with the floor and the need to maintain dynamic balance (Donker & Beek, 2002; Donker et al.). The results of the present study amplify the previous findings regarding the positive effect of walking velocity on coordinative stability by showing (through a combination of complementary measures, i.e., weighted coherence and the *SD* of the relative Fourier phase) that one can indeed attribute that effect to changes in relative phase dynamics, rather than changes in amplitude. The third deviant finding pertains to our main focus in the present study, namely, the effect of limb loading and asymmetry, and therefore calls for a more extensive discussion.

Theoretically, the different physical properties of the nonhomologous arm and leg introduce a frequency-detuning term ($\Delta\omega \neq 0$) that brings about a shift in a stable coordinative state or fixed point (Amazeen, Sternad, & Turvey, 1996; Daffertshofer et al., 1999; Treffner & Turvey, 1996). Several investigators have tested that theoretical insight empirically and shown that the coordination between symmetrical components or homologous limbs is more stable than that between asymmetrical components or nonhomologous limbs (e.g., Baldissera & Cavallari, 2001; Kelso & Jeka, 1992). Moreover, Jeka and Kelso (1995) and Serrien and Swinnen (1998) showed that, consistent with theoretical predictions, adding mass to the limbs influences the coordinative asymmetry. More specifically, loading an arm enhanced the coordinative symmetry between arm and leg movements in that the mean relative phase was closer to the intended relative phase relation (i.e., in- or antiphase) than it was in the unloaded condition, whereas loading a leg decreased the coordinative symmetry between arm and leg movements. In addition, it has been suggested that participants prefer to move their limbs at or near their natural frequency, resulting

in double swinging of the arms at very low walking velocities (e.g., Holt, Hamill, & Andres, 1990; Wagenaar & Van Emmerik, 2000). According to that interpretation, adding mass to the wrist may be thought of as a means to decrease the natural frequency of the arm, thereby reducing the difference from the physical properties of the leg and thus the range of walking velocities at which 2:1 frequency coordination between arm and leg movements is observed.

In the present study, however, the coordination between arm and leg movements remained unaffected by limb loading, in terms of both frequency and phase relations. More specifically, adding mass to both arms did not improve the coordinative symmetry between nonhomologous arm and leg movements and did not decrease the walking velocity at which a transition from 2:1 to 1:1 frequency coordination between arm and leg movements occurred, whereas adding mass to a single limb did not reduce the coordinative symmetry between homologous limb movements. The discrepancy between the present findings and those of Jeka and Kelso (1995) and Serrien and Swinnen (1998) may be explained in terms of the prevailing task constraints. Whereas maintaining overall postural balance is an essential requirement in walking, it was hardly an issue in Jeka and Kelso's and Serrien and Swinnen's experiments because their participants were seated. It may therefore well be the case that the neural organization underlying interlimb coordination during walking may be distinct from that in nonbalancing tasks, or at least that the coupling between central and peripheral control is modified as a result of altered sensory conditions. Furthermore, the arms are allowed to move freely during walking, whereas the leg movements are constrained by the requirement to propel the body forward by generating ground reaction forces through making alternating stepping movements. Thus, in the present study, the legs were constrained to move in antiphase, whereas the arms were not. In contrast, in Jeka and Kelso's and Serrien and Swinnen's experiments, the constraints on both the arm movements and the leg movements were identical. Furthermore, in the latter two studies, the participants were explicitly instructed to maintain a specific phase relation while moving at a particular movement frequency, whereas in the present experiment, no such instructions were given to the participants. We instructed them only to walk as naturally as possible on the treadmill (and to match the belt velocity). It is conceivable that during walking, the arm movements were coordinated with each other and with the leg movements so as to accommodate or facilitate the antiphase coordination between the leg movements required by the task, even in the presence of asymmetrical load perturbations. That possibility could explain why the load manipulation in the present experiment had no (or very little) effect on the observed patterns of interlimb coordination (Figure 5) and their stability (Figure 6; see also Figure 4), whereas it had a marked effect on the individual limb trajectories (Figure 2). An alternative explanation for those findings could be that the mass manipulations in the present experiment had little effect on the eigenfrequencies of the limbs because of the selected locations of wrist and ankle (cf. Van Soest, Peper, & Selles, 2004).

Most interesting, limb loading in the present study led to a decrease of the consistency of the individual limb trajectories without affecting their coordination, whereas increasing walking velocity led to a decrease in variability of both the individual limb trajectories and interlimb coordination. An important question is how the latter two effects (i.e., a decrease in variability of the individual limb movements and an increase in coordinative stability) are related. Does the decrease in the variability of the relative phasing between the limbs with increasing walking velocity result from the concomitant decrease in variability of the individual limb movements, or is it a genuine coordination effect reflecting stronger interlimb coupling? There are compelling reasons that the latter was the case, especially for the legs.

Because of biomechanical limitations in the ability of the musculoskeletal apparatus to increase step length and stride frequency (cf. Donker & Beek, 2002; Nilsson & Thorstensson, 1987), the leg movements and their coordination become more tightly constrained at higher walking velocities, and even more so in treadmill walking than in overground walking (cf. Dingwell, Cusumano, Cavanagh, & Sternad, 2001). Comparatively speaking, the impact of those constraints on the arm movements was probably much smaller, which might explain why the arm movements were more variable than the leg movements (Figure 2). It might also explain why the arm movements were more strongly affected than the leg movements by the added mass (Figure 2). Because of their freedom of movement, the arms may play an important role in accommodating the load perturbation as well as when the load is attached to the leg or legs, thus helping to preserve dynamic balance (cf. Donker & Beek, 2002). In an earlier study, Donker et al. (2002) showed that limb loading during walking strongly influences arm movements and arm muscle activity. Not only did arm muscle activity increase when load was added to the arm in question, it also increased when a leg or the other arm was loaded. That finding supports the possibility that the motor system may compensate the co-moving limbs for the load manipulations to meet the requirements of the task, that is, maintaining an energetically as well as dynamically optimal (i.e., stable) walking pattern.

The robustness of interlimb coordination during walking was illustrated further by the fact that no significant effects of loading on coordinative stability (be it quantified in terms of the *SD* of the various relative phase measures or relaxation time) were found in either the present study or in that of Jeka and Kelso (1995). However, Serrien and Swinnen (1998) found that adding a mass increased the *SD* of relative phase. They ascribed that deviant result to the fact that the frequencies used in the experiment of Jeka and Kelso were relatively high (1.00 to 2.25 Hz) as compared with the frequencies used in theirs (1.1 Hz). Like Jeka and Kelso, Serrien and Swinnen found that homologous limbs were

more strongly coupled than were nonhomologous limbs. Unlike Jeka and Kelso, however, they explained that finding by arguing that homologous limbs are more tightly coupled neurally than nonhomologous limbs are, leading to more effective compensatory processes. Those interpretations underscore the notion that a variety of constraints determine interlimb coordination.

In that context, and in view of the increasing number of studies on rhythmic interlimb coordination in a variety of tasks, Schöner's (1995) analysis of neural functioning in terms of distinguishable levels of behavioral components may be of interest. According to that analysis, the nervous system is organized in a functional, task-related way rather than in a structural, anatomy-related fashion. In consequence, the control structure for a given movement strongly depends on the nature of the task it serves. Schöner distinguished three levels of behavioral control: the goal level (at which the global, often spatially defined properties of the movement are stabilized, e.g., reaching toward a target by making a movement of a certain amplitude), the level of timing (at which, e.g., the relative timing between limb movements is stabilized), and the load level (at which movement patterns are stabilized against force perturbations). In everyday tasks, and under normal conditions, control is exerted at all three levels simultaneously. However, one may create special experimental circumstances to study one particular control level in isolation. For instance, when bimanual coordination tasks are performed by a seated individual, the requirement of maintaining balance plays only a modest role, and the mechanical interaction with the environment is small. Hence, there are almost no task constraints pertaining to the goal level or the load level, and the coordination dynamics could be attributed foremost to the timing level (cf., e.g., Post, Peper, & Beek, 2000). In walking, in contrast, the mechanical interaction with the environment (i.e., mechanical coupling between the limbs and discrete contact points with the floor) is an important factor requiring active control at the load level in addition to control at the timing level (i.e., relative phasing between limb movements) and at the goal level (i.e., keeping an upright orientation while propelling oneself forward in a desired direction of heading by pushing alternately with the feet against the ground).

In sum, the results of the present study indicate that the dynamical principles identified for bimanual interlimb coordination are not readily applicable to locomotion. In all likelihood, the reason for that difference is that walking is strongly determined by mechanical factors. To deepen our insight into the manner in which the dynamical properties of interlimb coordination during walking are shaped by those mechanical factors, it seems inevitable that we should build more encompassing models aimed at elucidating how those properties are instantiated in a neuromusculoskeletal system that interacts forcefully with the environment (see, e.g., Taga, 1995, for a useful step in that direction).

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